Reference: *Biol. Bull.* **166:** 127–139. (February, 1984)

VARIATION IN THE DIAPAUSE RESPONSE OF *LABIDOCERA AESTIVA* (COPEPODA: CALANOIDA) FROM DIFFERENT LATITUDES AND ITS IMPORTANCE IN THE EVOLUTIONARY PROCESS

NANCY H. MARCUS

Woods Hole Oceanographic Institution, Woods Hole, Massachusetts 02543

ABSTRACT

Labidocera aestiva were collected from three distantly separated sites along the Atlantic coast of the United States. Their offspring were reared in the laboratory under several combinations of photoperiod and temperature to assess the diapause response and genetic similarity of the populations. The results indicate that *L. aestiva* is not genetically homogeneous throughout its range. Differences in the percentage of subitaneous and diapause eggs produced by laboratory-reared and field-collected populations reflected the unique combination of environmental conditions occurring in the geographic regions from which the animals originated. In the Virginian province where planktonic stages of the species are seasonally present, diapause egg production is triggered by short day length photoperiods and cool temperatures. On the other hand in the Carolinian province where the planktonic stages tend to occur year-round diapause eggs are rarely produced by either field-collected females or their laboratory-reared offspring. This suggests that most of these animals lack the genetic capacity to produce diapause eggs. Diapause may lead to the reproductive isolation of populations if gene flow is reduced or prevented owing to their separation on a temporal scale.

INTRODUCTION

It has long been recognized that many marine planktonic organisms have very broad spatial distributions which often encompass an extensive latitudinal gradient (see discussions in Ekman, 1953; Raymont, 1963; Fleminger, 1975; Van der Spoel and Pierrot-Bults, 1979). This pattern has been attributed largely to their potential for passive dispersal across great distances in ocean currents. Despite evidence of phenotypic differences in morphological, behavioral, and/or physiological traits between populations from distant areas, marine biologists have argued that planktonic species are genetically homogeneous due to the potential for considerable panmixia (*i.e.*, random interbreeding of populations). Consequently, the observed phenotypic differences have often been ascribed to environmental modification. Progress in determining the basis for such variation has been hindered by difficulties encountered in obtaining, maintaining, and rearing planktonic species for genetic studies (Paffenhöfer and Harris, 1979). However, some insight into the genetic structure of planktonic populations has been gained from electrophoretic studies (*e.g.*, Manwell *et al.*, 1967; review by Gooch, 1975; Ayala and Valentine, 1979). An important outcome of these studies is that planktonic species are no longer regarded as necessarily being genetically homogeneous. A weakness with this approach, however, is that the adaptive significance of different electromorphs (*i.e.*, mobility variants revealed by electrophoresis) is often

Received 17 October 1983; accepted 17 November 1983.
Contribution No. 5513 from the Woods Hole Oceanographic Institution.

unknown. Thus, their importance in the evolutionary process and the formation of new species is difficult to assess. Studies that provide insight into the genetic divergence of traits of obvious adaptive significance should lead to a better understanding of the mechanism(s) which enable species to cope with environmental change, the potential importance of emigration in the re-population of foreign areas, and the evolutionary steps that are basic to speciation.

Labidocera aestiva is a calanoid copepod reported to occur in North American coastal waters from the Gulf of St. Lawrence to the Gulf of Mexico (Grice, 1956; Fleminger, 1957; Deevey, 1960; Cronin *et al.,* 1962; Anraku, 1964; Van Engel and Tan, 1965; Bowman, 1971; Turner *et al.,* 1979). In the northern portion of the range (*e.g.,* Vineyard Sound, Massachusetts) it is seasonally present in the plankton. Adults appear in mid-June and give rise to a series of generations stemming from subitaneous eggs which hatch within a few days of extrusion. By mid-December nauplii, copepodids, and adults disappear from the plankton, but the species maintains its presence in the area in the form of benthic diapause eggs (Marcus, 1979). Diapause eggs are produced during the fall, but do not hatch until the following spring. Thus, the first generation of animals that appears in June is derived from these diapause eggs. The ecological significance of the benthic diapause stage is that it enables survival of individuals during the periods that cannot be tolerated by the planktonic stages. The onset of diapause prevents the waste of partial generations. The termination of diapause synchronizes the life cycle of the species with the environmental regime so that development, growth, and reproduction are optimized. By rearing the offspring of females collected in Vineyard Sound, Massachusetts in the laboratory it has been shown that the type of egg produced by a female is triggered by a temperature-compensated photoperiodic response (Marcus, 1980a, b; 1982a, b). Short day lengths and cold temperatures are most effective in the induction of diapause eggs, whereas long day lengths and warm temperatures are more effective in the induction of subitaneous eggs. There is some variation among female *L. aestiva* in the particular combination of photoperiod and temperature which effectively triggers diapause egg production, and this variation helps to ensure survival of the species despite year to year fluctuations in environmental conditions.

The seasonal cycling of environmental conditions varies considerably along the latitudial gradient inhabited by *L. aestiva* resulting in longer periods of occurrence of populations in the plankton as one moves in a southerly direction. In Florida, where seasonal environmental fluctuations are small, the growth, development, and reproduction of *L. aestiva* in the plankton continues throughout the year (Bowman, 1971; Blades-Eckelbarger, pers. comm.). Published data on the temporal distribution pattern of the species along the coast (Deevey, 1960; Cronin *et al.,* 1962; Bowman, 1971; Lonsdale and Coull, 1977) indicates that the timing and/or expression of diapause may differ between populations. These differences could reflect either environmental modification of the phenotype or genetic differentiation.

This study was designed therefore to determine and compare the diapause response of populations of *L. aestiva* from different locations along the latitudinal gradient which makes up its range on the Atlantic coast of North America. The study used two approaches: 1) determination of the type(s) of eggs produced under a range of photoperiodic and temperature conditions by laboratory-reared offspring of different geographic heritages and 2) determination of the type(s) of eggs produced by freshly caught females from the field. The results indicate that the species is spatially subdivided into populations which differ in the expression of certain diapause traits and that these differences reflect genetic divergence. This differentiation exists despite the apparent potential for extensive transport and mixing of the planktonic stages in the

ocean currents. Diapause thus represents an adaptive response which may be of fundamental importance in the evolutionary process of speciation of some marine planktonic organisms.

Materials and Methods

Labidocera aestiva were collected from the plankton during a three-year period from September, 1979, to August, 1982, at four locations along the East coast of the United States: Delaware Bay, Delaware; Wachapreague Inlet, Virginia; Beaufort Inlet, North Carolina; and Fort Pierce Inlet, Florida. Samples were collected with 240 μm mesh plankton nets (mouth diameter either 0.25 or 0.75 m). The nets were either towed for five to ten minutes off a boat or in the case of some collections from Beaufort, the net was suspended off the Pivers Island bridge for several hours. The surface water temperature was determined at the time of each collection. In the laboratory adult *L. aestiva* were removed from the samples using a wide-mouth pipette and placed in large buckets containing filtered (5 micron) sea water. The contents were aerated and *Gymnodinium nelsoni* or *Artemia* nauplii were added to the containers as food. Within one to three days the animals were transported back to Woods Hole in insulated containers for experimental manipulation. In Beaufort and Fort Pierce, laboratory facilities were available at the Duke Marine Laboratory and Harbor Branch Foundation respectively, which made it possible to do the experimental analyses of the field-collected females within 24 hours of collection. If sufficient numbers of *L. aestiva* were present in the plankton samples, then some females were removed from the buckets, placed into small dishes containing filtered sea water and *Artemia* nauplii, and incubated overnight at room temperature (*i.e.*, 20°C–23°C). The following day eggs were collected and transferred to another dish containing filtered sea water. The eggs were examined after 2 to 3 days to determine the number that had hatched. After five days unhatched eggs were placed into glass screw-capped jars containing filtered sea water and chilled at 5°C in a refrigerator. These jars were transported back to Woods Hole and subsequently maintained at 5°C. After chilling for a minimum of 4 weeks the jars were warmed at 19°C or 25°C and the number of eggs that hatched after this treatment was determined. The adults which were transported back to Woods Hole were maintained for as long as possible in the laboratory, in either buckets or 19 liter glass carboys. The buckets were provided with airstones, whereas the carboys were mounted on a mechanical rotator. In both cases the animals were provided with a mixed diet of four dinoflagellates: *Gymnodinium nelsoni, Prorocentrum micans, Gonyaulax polyedra,* and *Scrippsiella trochoideum* (previously referred to as *Peridinium trochoideum*). These field-collected animals were used to initiate most experimental cultures. Females were transferred from the buckets or carboys into dishes containing filtered sea water. They were fed *Gymnodinium nelsoni* and incubated overnight at 19°C. The next day eggs were collected and incubated for two more days at 19°C. Hatched nauplii were placed into 19 liter glass carboys and reared to reproductive maturity as described previously for animals from Vineyard Sound (Marcus, 1980a, b). The carboys were mounted on a mechanical plankton rotator in an environmental chamber equipped with light cycling and temperature controls. The responses to nine different combinations of temperature (14.5°C, 18.0°C, 24.0°C) and photoperiod regime (18L–6D, 12L–12D, 8L–16D) were examined as was done previously for the animals from Vineyard Sound (Marcus, 1980a, 1982b). The temperature fluctuated ±1°C throughout the 24-hour cycle. Delaware Bay animals were also reared at one additional set of environmental conditions (*i.e.*, 10L–14D at 18°C). Due to equipment problems, the temperature level occasionally exceeded the

set point by several degrees. Such failures were remedied within 24 hours and only rarely resulted in the mass mortality of animals in the experimental carboys. On these occasions new cultures were started to obtain the necessary data. Breakdowns also affected some of the algal cultures used for feeding so that periodically the diet had to be modified to include more or less one of the food species. Every effort was made to initiate experiments from the eggs of field-collected adults or the second generation offspring (to reduce the possible effects of selection due to laboratory conditions). This was not always possible due to the difficulties encountered in obtaining animals from the different sites. Thus a few experiments were started from the eggs of third generation animals, and one (D11) was based on those of fourth generation animals. For all experiments the same schedule of feeding, transfer of animals to clean sea water, and egg collection reported by Marcus (1980a, 1982b) was followed in this study. Also the types of eggs which were produced were determined for each set of conditions according to the criteria of Marcus (1982b).

Results

Seasonal field data: adult abundance and temperature conditions

The location of the four sites sampled in this study and the Vineyard Sound site sampled by Marcus (1979, 1980a, 1982a, b) are shown in Figure 1. *L. aestiva* was first obtained from Fort Pierce in September, 1979. Thereafter animals were obtained in April, 1980, 1981; January, 1981; February, 1981, 1982; August, 1981; and September, 1981. The surface water temperature ranged from 17°C in January to 27°C in August and September. Although the spatial distribution of *L. aestiva* was somewhat patchy in this area (*i.e.,* sometimes a tow would have no *L. aestiva,* yet moving to another spot yielded hundreds to thousands) adults were always abundant. This is a qualitative description of the samples as the methods of collection were not designed for a quantitative analysis. On the other hand, *L. aestiva* were not so readily obtained in Beaufort. A sampling trip in April 1981 yielded only a few adults. Adults were successfully collected in July, 1981, November, 1981, and August, 1982, but never in the quantities encountered at Ft. Pierce. The surface water temperature ranged from 13°C in April to 30°C in July. Considerable difficulty was encountered in obtaining *L. aestiva* in Wachapreague Inlet. Numerous tows taken in November, 1981, yielded no animals. The water temperature was 11°C. In June, 1982, *L. aestiva* adults were still not abundant, although some copepodites were present. The water temperature was 20°C. In July, 1982, adults again were not obtained. Thus, in July, 1982, Delaware Bay was chosen as a new study site. Several tows were taken and by pooling their contents hundreds of females were obtained. The water temperature at this time was 22°C. We returned to this location in August, 1982, but were unable to obtain sufficient animals. Thus all experimental manipulations for Delaware Bay were based on the one collection of July, 1982.

Egg production by field-collected and laboratory-reared females

Offspring of Delaware Bay, Beaufort, and Fort Pierce heritages were successfully reared through reproductive maturity under all of the combinations of photoperiod and temperature tested. The percentages of eggs that hatched after the initial incubation at 25°C and that which hatched after prolonged exposure to 5°C are shown for each carboy in Tables I, II, and III. F values derived from an analysis of variance for the arc-sin transformed data indicate no significant difference between the means of replicate carboys for 23 of the 28 combinations tested. The average percentages of

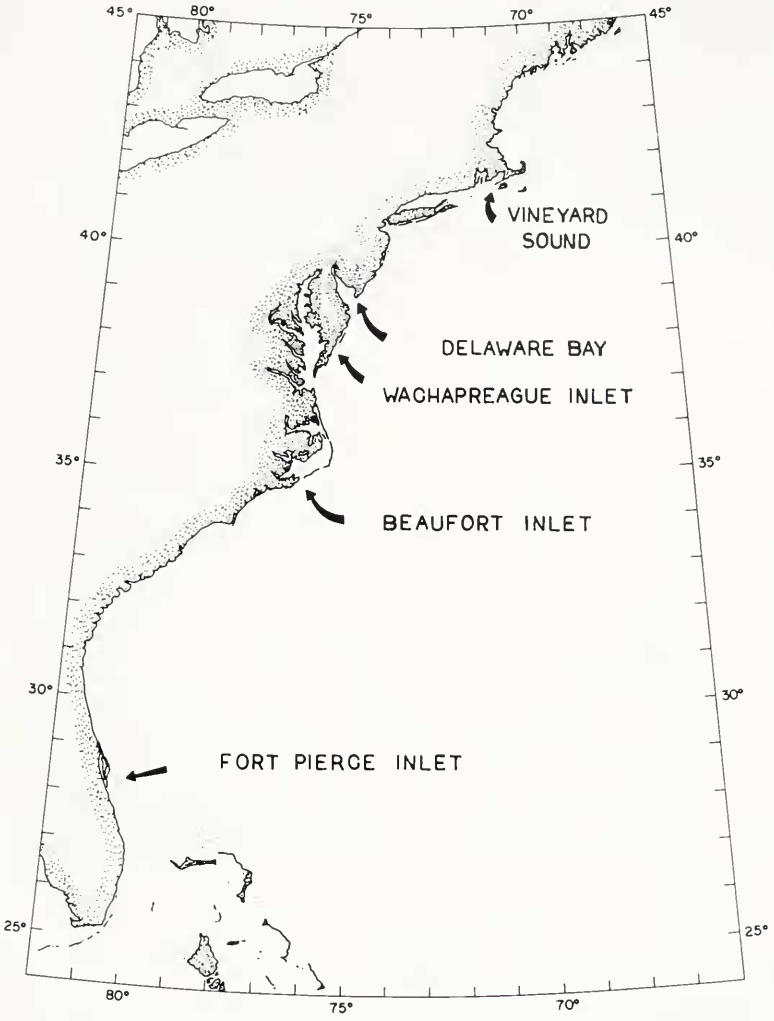

FIGURE 1. Location of study sites.

subitaneous, diapause, and non-viable eggs at each photoperiodic and temperature regimen are summarized in Figure 2.

Laboratory-reared females of Ft. Pierce heritage rarely produced diapause eggs (less than 2.0% of all eggs produced) even under the short day length and cool temperatures that favor their production by Vineyard Sound animals (data of Marcus, 1980a, 1982b). Similarly, diapause eggs were rarely obtained from the field-collected specimens.

Animals of Beaufort heritage responded differently. Diapause eggs were obtained from laboratory-reared females under short day length conditions, but not consistently, and not in large numbers (*e.g.,* 6.0%). Diapause eggs (*ca.* 22.0%) were produced by females collected in the field during November, 1981.

The diapause response of laboratory-reared females of Delaware Bay heritage was quite different from the Beaufort and Ft. Pierce populations. Diapause eggs were

TABLE I

*Percent hatch of eggs produced by females reared at 13.5°–15.5°C under 8L–16D, 12L–12D, or 18L–6D**

	DELAWARE			BEAUFORT			FT. PIERCE		
Photo-period	Carboy no.	Initial 25°C	Final 5°C	Carboy no.	Initial 25°C	Final 5°C	Carboy no.	Initial 25°C	Final 5°C
8L–16D	$D1^1$	27.8 ± 8.2	80.8 ± 10.1	$B1^3$	90.7 ± 2.5	—	$F1^1$	79.5 ± 2.4	—
	$D2^1$	27.2 ± 9.1	79.6 ± 8.4	$B2^2$	86.1 ± 5.0	—	$F2^1$	86.4 ± 4.4	—
	$D3^1$	27.4 ± 7.7	84.3 ± 10.9						
X		27.5 ± 0.2	81.5 ± 1.4		88.4 ± 2.3	—		83.0 ± 3.5	
12L–12D	$D4^3$	80.3 ± 8.3	40.0 ± 25.1	$B3^1$	78.5 ± 8.2	13.8 ± 8.0	$F3^1$	85.8 ± 2.2	—
	$D5^3$	84.8 ± 2.6	16.0 ± 11.3	$B4^2$	72.7 ± 10.2	0.0	$F4^3$	87.9 ± 1.9	0.0
				$B5^2$	74.1 ± 13.7	0.0			
X		82.6 ± 2.3	22.0 ± 6.8		75.1 ± 1.8	4.6 ± 4.6		86.9 ± 1.1	
18L–6D	$D6^2$	79.3 ± 6.4	0.0	$B6^{3**}$	86.8 ± 2.2	1.3 ± 2.3	$F5^1$	81.8 ± 1.6	—
	$D7^2$	79.5 ± 6.6	0.0	$B7^{3**}$	76.2 ± 1.3	2.8 ± 3.8	$F6^2$	84.9 ± 2.5	3.0 ± 2.7
				$B8^{1**}$	88.3 ± 3.8	3.3 ± 6.5	$F7^2$	87.4 ± 3.3	6.0 ± 4.6
X		79.4 ± 0.1	0.0		83.8 ± 3.8	2.4 ± 0.6		84.7 ± 1.6	4.5 ± 1.5

* Eggs that did not hatch within 4–5 days at 25°C (initial) were incubated in jars at 5°C. The final hatch of these eggs at 25°C is indicated. D = Delaware, B = Beaufort, and F = Fort Pierce. Superscripts refer to 1, 2, 3, or 4 generation offspring. X = mean ± S.E.

** Significant difference at .05 level.

TABLE II

*Percent hatch of eggs produced by females reared at 17.0°–19.0°C under 8L–16D, 10L–14D, 12L–12D, or 18L–6D**

	DELAWARE			BEAUFORT			FT. PIERCE		
Photo-period	Carboy no.	Initial 25°C	Final 5°C	Carboy no.	Initial 25°C	Final 5°C	Carboy no.	Initial 25°C	Final 5°C
8L–16D	D8[1]	20.0 ± 2.9	84.0 ± 7.8	B9[1]	90.3 ± 3.3	—	F8[2]	84.5 ± 4.5	9.0 ± 15.6
	D9[1]	23.7 ± 7.0	78.3 ± 14.2				F9[2]	80.3 ± 3.1	2.3 ± 4.0
	D10[1]	19.4 ± 6.8	80.6 ± 7.6						
X		21.0 ± 1.3	81.0 ± 1.7					82.4 ± 2.1	5.7 ± 3.3
10L–14D	D11[4]	44.3 ± 11.4	83.0 ± 6.4						
	D12[2]	54.0 ± 10.4	59.8 ± 13.3						
X		49.2 ± 4.9	71.4 ± 11.6						
12L–12D	D13[3]	93.3 ± 1.3	—	B10[2]	78.8 ± 3.4	9.0 ± 10.2	F10[1]**	77.8 ± 4.3	—
	D14[3]	91.8 ± 3.4	—	B11[2]	79.6 ± 3.1	24.0 ± 0.0	F11[2]**	92.7 ± 2.1	15.0 ± 21.2
X		92.6 ± 0.8	—		79.2 ± 0.4	16.5 ± 7.5		85.3 ± 7.5	
18L–6D	D15[2]	93.4 ± 2.5	—	B12[1]	88.7 ± 2.7	—	F12[1]**	71.7 ± 2.9	1.3 ± 2.5
	D16[2]	95.8 ± 1.3	—	B13[1]	85.8 ± 2.5	—	F13[1]**	87.7 ± 4.0	0.0
X		94.6 ± 1.2	—		87.3 ± 1.5	—		79.7 ± 8.0	0.6 ± 0.6

* Refer to Table I for explanation of hatch data and symbols.
** Significant difference at .05 level.

TABLE III

*Percent hatch of eggs produced by females reared at 23.0°–25.0°C under 8L–16D, 12L–12D, or 18L–6D**

	DELAWARE			BEAUFORT			FT. PIERCE		
Photo-period	Carboy no.	Initial 25°C	Final 5°C	Carboy no.	Initial 25°C	Final 5°C	Carboy no.	Initial 25°C	Final 5°C
8L–16D	D17[3]**	69.0 ± 11.0	81.4 ± 11.3	B14[1]	74.8 ± 16.0	57.3 ± 29.1	F14[2]	86.5 ± 7.3	—
	D18[3]**	83.3 ± 2.6	24.8 ± 14.3	B15[1]	81.3 ± 3.7	54.7 ± 10.1	F15[3]	86.3 ± 5.1	7.5 ± 10.6
				B16[1]	82.1 ± 4.8	10.0 ± 17.3	F16[3]	80.8 ± 11.0	0.0
				B17[1]	87.5 ± 0.1	0.0			
X		76.2 ± 7.2	53.1 ± 28.3		81.4 ± 2.6	30.5 ± 14.9		84.5 ± 1.9	3.8 ± 3.8
12L–12D	D19[2]	76.3 ± 11.2	84.2 ± 13.9	B18[2]	90.7 ± 3.2	—	F17[1]	89.0 ± 1.0	—
	D20[2]	80.8 ± 11.1	89.0 ± 6.0	B19[2]	87.7 ± 1.5	—	F18[1]	89.7 ± 4.2	—
X		78.6 ± 2.3	85.6 ± 1.4		89.2 ± 1.5	—		89.4 ± 0.4	—
18L–6D	D21[2]**	79.0 ± 4.0	2.0	B20[2]	92.1 ± 3.8	—	F19[1]	88.4 ± 1.0	—
	D22[2]**	62.3 ± 2.1	0.0	B21[3]	89.0 ± 2.1	0.0	F20[1]	83.6 ± 4.5	—
							F21[1]	81.1 ± 5.8	—
X		70.7 ± 8.4	0.0		90.6 ± 1.6	—		84.4 ± 2.1	—

* Refer to Table 1 for explanation of hatch data and symbols.
** Significant difference at .05 level.

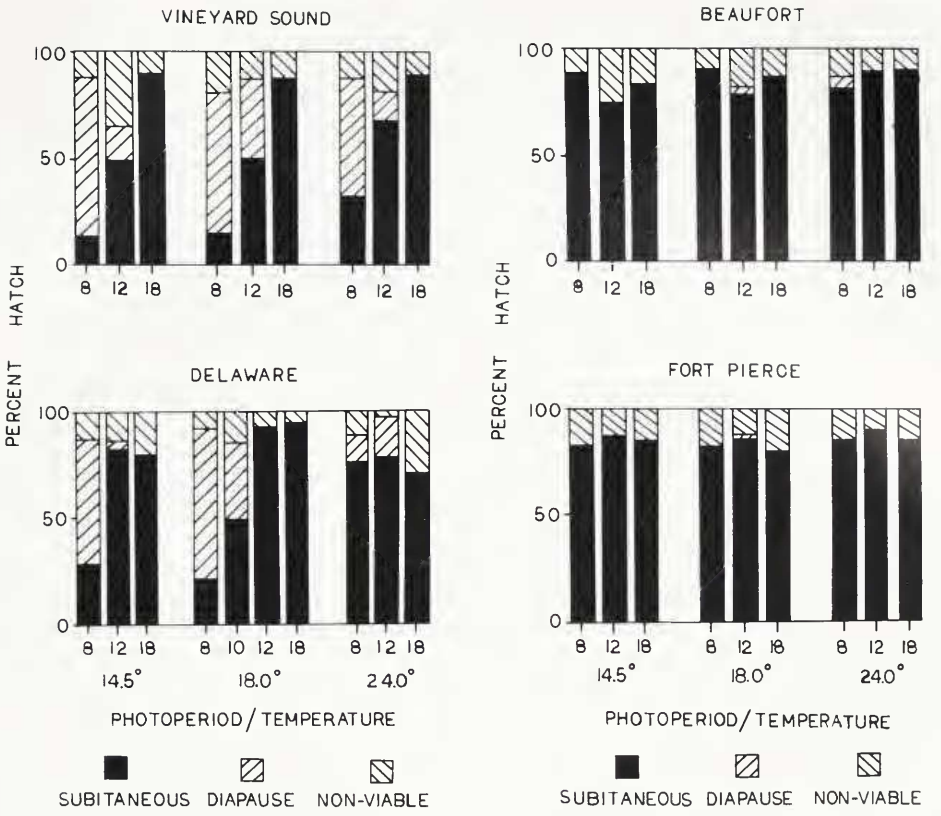

FIGURE 2. Subitaneous, diapause, and non-viable egg production (percent) by females reared under 8L–16D, 10L–14D, 12L–12D, or 18L–6D at 14.5°C, 18.0°C, or 24.0°C (±1.0°C). a) Vineyard Sound and Delaware Bay, b) Beaufort and Fort Pierce. Data for Vineyard Sound from Marcus (1980a, 1982b).

consistently produced by these females. Females that were collected from the field in July did not produce diapause eggs. For Delaware Bay animals reared in the laboratory, short day lengths were most effective in the induction of diapause egg production. Although a 12L–12D photoperiod at 18°C did not result in a marked decline of subitaneous egg production compared to 18L–6D, a decline in subitaneous and an increase in diapause egg production was obtained by rearing the animals at 10L–14D at this temperature. The percentage of non-viable eggs produced ranged from 3.0% to 29.3% for the entire study, but most values were less than 15.0%.

DISCUSSION

The results of this study demonstrate that *L. aestiva* is not genetically homogeneous throughout its range, but rather is composed of distinct populations genetically adapted to local environmental conditions. Within each region the critical photoperiod for diapause induction expressed by the population has been adjusted by natural selection to maximize growth of the species. Due to latitudinal variation in climatic (*e.g.*, temperature, Bumpus, 1957) and day length conditions (U. S. Dept. of Commerce, 1983), disruptive selection has promoted differentiation of populations along the north-south gradient. This divergence has occurred despite the potential for gene flow via transport of planktonic stages in ocean currents.

The general lack of diapause egg production by females collected from Ft. Pierce waters as well as from their laboratory-reared offspring strongly suggests that most of these animals do not have the genetic capacity to produce diapause eggs. This seems reasonable since diapause eggs would not be as important for survival in this region owing to the species year-round presence in the plankton (P. Blades-Eckelbarger, pers. comm.). The basis of the significant variation that exists among the replicate carboys at 18°C, 12L–12D and 18°C, 18L–6D is not known. In both cases one carboy yielded unexpectedly lower subitaneous egg production (77.8% and 71.7%, respectively) than the other duplicate culture (92.7% and 87.7%, respectively). However, the replicates for each set were reared at the same time and were exposed to the identical environmental regimen and diet. The cultures were also started from the eggs of field-collected adults or their first generation offspring so that inbreeding is an unlikely cause.

In the Beaufort region *L. aestiva* adults have been reported year-round as well, although their abundance fluctuates seasonally (Sutcliffe, 1950; Bowman, 1971). The species is widespread across the shelf in the winter and spring, but restricted to the coast in the summer and fall (Bowman, 1971). However, Sutcliffe (1950) indicated that the species was present only on occasion in the Beaufort Inlet. The results of the laboratory rearing studies reflect these seasonal patterns. Since diapause eggs were not consistently obtained under short day length conditions in the laboratory it seems likely that only a small portion of the females occurring in the Beaufort region have the genetic capacity to produce diapause eggs. Thus if the animals used to start an experiment had the genetic capacity to produce diapause eggs, then such eggs would be produced by their offspring under the expected short day length regimens in the laboratory. However, if the animals lacked the genetic capacity then regardless of the environmental conditions imposed in the laboratory only subitaneous eggs would be produced. If the frequency of individuals possessing the genetic capacity to produce diapause eggs is small, this would account for the inconsistent results obtained in the laboratory. The significant variation that is evident among the cultures reared at 14.5°C, 18L–6D may be due to the fact that carboys B6 and B7 were third generation offspring, but B8 was a first generation culture. However, a similar comparison between F3 (first generation) and F4 (third generation) from Ft. Pierce at 14.5°C, 12L–12D is not significant. There were no difficulties with the incubator conditions or with the algal cultures used in the diet when these experiments were conducted.

The occurrence of diapause egg production in the populations from the Carolinian Province contrasts with that observed for populations in the Virginian Province from Delaware Bay (this study) and from Vineyard Sound (Marcus, 1980a, 1982b). The particular response of the population from Delaware Bay reflects the need for a diapause stage to cope with the harshness of winter as is the case for the animals that occur in Vineyard Sound. However, in the more southern locality (*i.e.,* Delaware Bay) favorable conditions for growth, development, and reproduction persist for a great portion of the year. In this region planktonic stages are present from May to January (Deevey, 1960; Cronin *et al.,* 1962). Since *L. aestiva* were collected from Delaware Bay only during the month of July in this study, it is not known at what time during the fall diapause egg production begins. As expected, diapause eggs were not obtained from females collected in July. To take advantage of the longer growing season, it is likely that diapause egg production does not begin in September as in Vineyard Sound, but rather is delayed by one to two months. From October to November in the Delaware Bay region the period of day length ranges from about 11.75 to 10.5 hours (U. S. Dept. of Commerce, 1983). Thus photoperiodic cycles somewhere in this range should result in diapause egg production by Delaware Bay

animals, but not a 12L–12D cycle. These predictions are supported by the laboratory results as evidenced by the still high levels of subitaneous egg production by Delaware Bay animals at 12L–12D, at 18°C. Only with the intermediate photoperiodic cycle of 10L–14D was diapause egg production markedly increased.

The diapause responses expressed by the laboratory-reared and field populations of *L. aestiva* from the different latitudes are similar to those of many insect species. For these animals as for *L. aestiva* the critical day length (*i.e.,* that which induces greater than 50% diapause) tends to be longer in northern populations than in southern populations. The divergence among insect species is most for those species which have a limited capacity for dispersal and migration (see Danilevsky, 1965; Dingle, 1978; Beck, 1980; Denno and Dingle, 1981; Dingle and Hegmann, 1982). Thus, for *L. aestiva,* either such dispersal does not exist or selection overrides the homogenizing effects of any gene flow that may occur. The females that occur in Vineyard Sound, but do not produce diapause eggs (Marcus, 1982a) may be indicative of genetic input from southern regions (*e.g.,* Ft. Pierce) via the hybridization of individuals. That such mixing may occur in the field is suggested by the successful interbreeding of copepods from Vineyard Sound and Ft. Pierce in the laboratory (Marcus, unpub.). Such mixing in the field should promote variability within the populations as suggested by Marcus (1982a).

It is commonly held that the formation of new species reflects the accumulation of genetic differences (Mayr, 1963). But how much or what kind of differentiation is necessary to achieve this distinction is not understood (see Milkman, 1982). It is assumed that genetic adaptation to spatial variation and isolation by distance are of primary importance to the process, but an additional factor which may be important is adaptation to temporal variation (Mayr, 1963; Tauber and Tauber, 1977). In his paper on the paradox of the plankton, Hutchinson (1961) suggests that the rich species diversity of planktonic communities in a seemingly homogeneous realm could be attributed to temporal heterogeneity. In other words, by partitioning the environment on a temporal scale, differences in the timing of occurrence of individuals may reduce competition and enable more species to exist in a given area. Although we no longer regard the marine planktonic system as spatially homogeneous, temporal heterogeneity provides an additional dimension for divergence to occur. If so, then the existence of mechanisms that synchronize the timing of life cycle phases with the environmental regime must be crucial to the survival of species. Some of these mechanisms may be life history adaptations that ensure the accurate coordination of development, growth, and reproduction with favorable periods in the environment and conversely the coupling of periods of dormancy, migration, and dispersal with unfavorable periods. Danilevsky (1965) and Tauber and Tauber (1981) rank diapause as the most important factor contributing to the synchronization of insect life cycles, and this may well be true for many marine planktonic organisms. The diapause response may lead to the reproductive isolation of populations if gene flow is reduced or prevented due to their separation on a temporal scale. Thus the timing of the appearance and disappearance of life history phases resulting from diapause may be of fundamental importance in the speciation process.

ACKNOWLEDGMENTS

I thank the Directors and other very helpful people at the Harbor Branch Foundation, Fort Pierce, Florida; Duke University Marine Laboratory, Beaufort, North Carolina; Virginia Institute of Marine Science, Wachapreague, Virginia; and the University of

Delaware, Lewes, Delaware for providing the necessary laboratory facilities and research vessels. Particular thanks are extended to M. Castagna, P. Blades-Eckelbarger, C. Epifanio, C. Jacoby, J. Ramus, and M. Youngbluth. Also, I. Bosch, K. Chipperfield, and C. Fuller provided valuable assistance with the laboratory manipulations in Woods Hole. T. Cowles and G. Grice offered helpful criticism of the manuscript. Supported by NSF Grant OCE80-24440.

LITERATURE CITED

ANRAKU, M. 1964. Influence of the Cape Cod Canal on the hydrography and on the copepods in Buzzards Bay and Cape Cod Bay, Massachusetts. I. Hydrography and distribution of copepods. *Limnol. Oceanogr.* **9:** 46–60.

AYALA, F., AND J. VALENTINE. 1979. Genetic variability in the pelagic environment: a paradox? *Ecology* **60:** 24–29.

BECK, S. 1980. *Insect Photoperiodism.* Academic Press, New York. 387 pp.

BOWMAN, T. 1971. The distribution of calanoid copepods off the south-eastern United States between Cape Hatteras and southern Florida. *Smithsonian Contributions to Zoology,* No. 96. 58 pp.

BUMPUS, D. 1957. Surface water temperatures along Atlantic and Gulf coasts of the United States. *U. S. Fish and Wildlife Service-Spec. Sci. Rep,* No. 214. 153 pp.

CRONIN, L., J. DAIBER, AND E. HULBERT. 1962. Quantitative seasonal aspects of zooplankton in the Delaware River estuary. *Chesapeake Sci.* **3:** 63–93.

DANILEVSKY, A. 1965. *Photoperiodism and Seasonal Development of Insects,* 1st English Edition. Oliver and Boyd, Edinburgh.

DEEVEY, G. 1960. The zooplankton of the surface waters of the Delaware Bay region. *Bull. Bingham Oceanogr. Coll.* **17:** 5–53.

DENNO, R., AND H. DINGLE, eds. 1981. *Insect Life History Patterns, Habitat and Geographic Variation.* Springer-Verlag, New York. 225 pp.

DINGLE, H., ed. 1978. *Evolution of Insect Migration and Diapause.* Springer-Verlag, New York. 284 pp.

DINGLE, H., AND J. HEGMANN, eds. 1982. *Evolution and Genetics of Life Histories.* Springer-Verlag, New York. 250 pp.

EKMAN, S. 1953. *Zoogeography of the Sea.* Sidgwick and Jackson Ltd., London. 417 pp.

FLEMINGER, A. 1957. New calanoid copepods of *Pontella* Dana and *Labidocera* Lubbock with notes on the distribution of genera in the Gulf of Mexico. *Tulane Stud. Zool.* **5:** 19–34.

FLEMINGER, A. 1975. Geographical distribution and morphological divergence in American coastal zone planktonic copepods of the genus *Labidocera. Estuarine Res.* **1:** 394–419.

GOOCH, J. 1975. Mechanisms of evolution and population genetics in the sea. Pp. 349–409 in *Marine Ecology,* D. Kinne, ed. Wiley Interscience, New York.

GRICE, G. 1956. A qualitative and quantitative seasonal study of the copepods of Alligator Harbor. Florida State University Studies, No. 22. *Pap. Oceanogr. Inst.* **2:** 37–70.

HUTCHINSON, G. E. 1961. The paradox of the plankton. *Am. Nat.* **95:** 137–146.

LONSDALE, D., AND B. COULL. 1977. Composition and seasonality of zooplankton of North Inlet, South Carolina. *Chesapeake Sci.* **19:** 272–283.

MANWELL, C., C. BAKER, P. ASHTON, AND E. CORNER. 1967. Biochemical differences between *Calanus finmarchicus* and *C. helgolandicus. J. Mar. Biol. Assoc. U. K.* **47:** 145–169.

MARCUS, N. 1979. On the population biology and nature of diapause of *Labidocera aestiva* (Copepoda:Calanoida). *Biol. Bull.* **157:** 297–305.

MARCUS, N. 1980a. Photoperiodic control of diapause in the marine calanoid copepod, *Labidocera aestiva* (Copepoda:Calanoida). *Biol. Bull.* **159:** 311–318.

MARCUS, N. 1980b. Diapause and the evolution of marine copepods. *Am. Zool.* **20:** 779.

MARCUS, N. 1982a. The reversibility of subitaneous and diapause egg production by individual females of *Labidocera aestiva* (Copepoda:Calanoida). *Biol. Bull.* **162:** 39–44.

MARCUS, N. 1982b. Photoperiodic and temperature regulation of diapause in *Labidocera aestiva* (Copepoda:Calanoida). *Biol. Bull.* **162:** 45–52.

MAYR, E. 1963. *Animal Species and Evolution.* Belknap Press, Cambridge, Massachusetts. 797 pp.

MILKMAN, R., ed. 1982. *Perspectives on Evolution.* Sinauer Associates, Sunderland. 241 pp.

PAFFENHÖFER, G., AND R. HARRIS. 1979. Laboratory culture of marine holozooplankton and its contribution to studies of marine planktonic food webs. *Adv. Mar. Biol.* **16:** 211–308.

RAYMONT, J. 1963. *Plankton and Productivity in the Oceans.* McMillan Company, New York. 660 pp.

SUTCLIFFE, W. 1950. *A Qualitative and Quantitative Study of Surface Zooplankton at Beaufort, North Carolina.* Ph.D. Thesis, Duke University, Durham, North Carolina.

TAUBER, C., AND M. TAUBER. 1977. A genetic model for sympatric speciation through habitat diversification and seasonal isolation. *Nature* **268:** 702–705.

TAUBER, C., AND M. TAUBER. 1981. Insect seasonal cycles: Genetics and evolution. *Ann. Rev. Ecol. Syst.* **12:** 281–308.

TURNER, J., S. COLLARD, J. WRIGHT, D. MITCHELL, AND P. STEELE. 1979. Summer distribution of pontellid copepods in the neuston of the eastern Gulf of Mexico continental shelf. *Bull. Mar. Sci.* **29:** 287–297.

United States Department of Commerce. 1983. *Tide tables, East coast of North and South America.* U. S. Government Printing Office, Washington, DC. 285 pp.

VAN DER SPOEL, S., AND A. PIERROT-BUTTS, eds. 1979. *Zoogeography and Diversity of Plankton.* John Wiley and Sons, New York. 410 pp.

VAN ENGEL, W., AND E. TAN. 1965. Investigations of inner continental shelf waters off Lower Chesapeake Bay. Part VI. The copepods. *Chesapeake Sci.* **6:** 183–189.